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PREDATION OF ARTIFICIAL GROUND NESTS ON WHITE-TAILED PRAIRIE DOG COLONIES

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Abstract: Prairie dog (*Cynomys* spp.) colonies are unique to prairie and shrub-steppe landscapes. However, widespread eradication, habitat loss, and sylvatic plague (*Yersinia pestis*) have reduced their numbers by 98% since historical times. Birds associated with prairie dogs also are declining. Potential nest predators, such as coyotes (*Canis latrans*), swift foxes (*Vulpes velox*), and badgers (*Taxidea taxus*), may be attracted to colonies where a high concentration of prairie dogs serve as available prey. Increased abundance of small mammals, including prairie dogs, also may increase the risk of predation for birds nesting on colonies. Finally, because grazing by prairie dogs may decrease vegetation height and canopy cover, bird nests may be easier for predators to locate. In this study, we placed 1,444 artificial ground nests on and off 74 white-tailed prairie dog (*C. leucurus*) colonies to test the hypothesis that nest predation rates are higher on colonies than at nearby off sites (i.e., uncolonized habitat). We sampled colonies from 27 May to 16 July 1997 at the following 3 complexes: Coyote Basin, Utah and Colorado; Moxa Arch, Wyoming; and Shirley Basin, Wyoming. Differences in daily predation rates between colonies and paired off sites averaged 1.0% ($P = 0.060$). When converted to a typical 14-day incubation period, predation rates averaged 14% higher on colonies ($57.7 \pm 2.7\%$; $\bar{x} \pm \text{SE}$) than at off sites ($50.4 \pm 3.1\%$). Comparisons of habitat variables on colonies to off sites showed percent canopy cover of vegetation was similar ($P = 0.114$), percent bare ground was higher on colonies ($P < 0.001$), Robel cover (i.e., visual obscuration of vegetation) was lower on colonies ($P < 0.001$), and density of active burrows was higher on colonies ($P < 0.001$). However, none of these habitat variables was correlated with differences in predation rates ($P > 0.288$). Although we found the risk of nest predation was higher on white-tailed prairie dog colonies than at off sites, fitness of birds nesting on colonies might depend on other factors that influence foraging success, reproductive success, or nestling survival.

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Key words: artificial nests, Colorado, *Cynomys leucurus*, ground-nesting birds, predation, shortgrass prairie, shrub-steppe, Utah, vegetation, white-tailed prairie dog, Wyoming.

Prairie dogs have been described as a key-stone species in western North America (Miller et al. 1994). Before European settlers altered the land, all 5 species of prairie dogs may have occupied 41 million ha (Anderson et al. 1986), but habitat loss from conversion of land to agriculture, direct poisoning of prairie dogs to reduce competition with livestock, and the spread of sylvatic plague have reduced their distribution by perhaps 98% (Marsh 1984). Avian species associated with prairie dogs also have declined, including a host of grassland and shrub-steppe birds (Knopf 1996). Many prairie birds, such as the mountain plover (*Charadrius montanus*), killdeer (*Charadrius vociferus*), horned lark (*Eremophila alpestris*), and McCown's

longspur (*Calcarius mccownii*) nest on the ground in prairie dog colonies.

Higher densities of predators on prairie dog colonies may place nests at a greater risk of predation. Krueger (1986) suggested the density of medium-sized predators, such as coyotes, swift foxes, and badgers, was 5.7 times higher on colonies than at off sites. Small mammals also are efficient predators of bird eggs (Cannings and Threlfall 1981) and can reach even higher numbers on colonies (Agnew et al. 1986). Deer mice (*Peromyscus maniculatus*) and northern grasshopper mice (*Onychomys leucogaster*) were nearly 3 times more abundant on colonies than at off sites in an Oklahoma study (O'Meilia et al. 1982). Another suggested nest predator is the prairie dog itself, although supporting data are lacking (Mickey 1943). Finally, avian nest

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predators may find nests on colonies easier to locate (Creighton and Porter 1974).

Nests on colonies may be easier for predators to locate because the vegetation is typically shorter and less dense. Prairie dogs remove vegetation through herbivory and, presumably, to increase visibility for predator detection (Clark 1977, Hoogland 1995). This contrast between a colony and its surrounding area creates edge, and edge can increase nest predation (Yahner 1996, Fenske-Crawford and Niemi 1997). For example, studies in fragmented tallgrass prairies (Burger et al. 1994) show higher predation rates near edges and in smaller fragments. In western shrub-steppe habitats, vegetation structure is an important predictor of predation rates for artificial sage grouse (*Centrocercus urophasianus*) nests (DeLong et al. 1995).

Our objective was to evaluate nest predation of ground-nesting birds on white-tailed prairie dog colonies. Specifically, we asked the following questions: (1) was nest predation higher on colonies than at nearby off sites?; (2) were differences in vegetative cover or prairie dog burrow density good predictors of differences in nest predation rates?; (3) how did type of disturbance to eggs and nests differ on and off colonies?; and (4) did evidence suggest prairie dogs may be nest predators? For this study, we used artificial nests to simulate natural nests of ground-nesting birds. We assumed differences in predation rates of artificial nests placed on and off colonies were a reasonably accurate index to differences in predation rates of natural nests (Major and Kendal 1996). Except where noted, we assumed nest disturbance was the result of attempted or successful nest predation.

STUDY AREA

White-tailed prairie dogs occur throughout the shrub-steppe and western shortgrass prairie ecosystems in the Rocky Mountain region (Fig. 1), although occupied habitat within this area varies greatly. In the east, low-growing shrubs and native grasses support McCown's longspurs, mountain plovers, and horned larks. In the west, Brewer's sparrows (*Spizella breweri*), sage sparrows (*Amphispiza belli*), and horned larks are common on or near prairie dog colonies.

To represent this variation and broaden our inferential ability, we selected our study colonies from 3 major complexes (a complex is an aggregation of colonies; Biggins et al. 1993) across the range of the white-tailed prairie dog

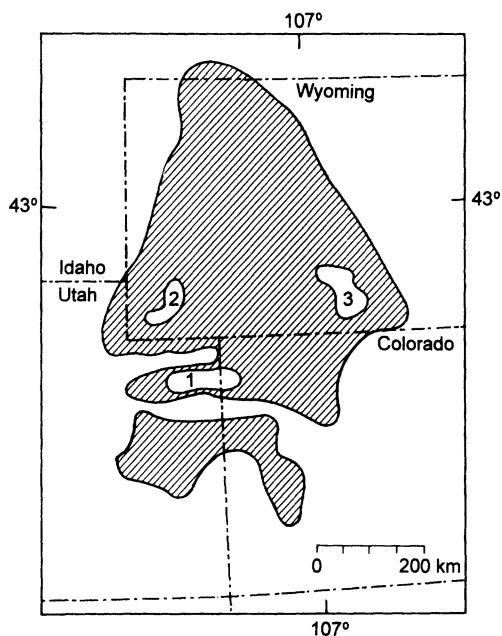


Fig. 1. Range of the white-tailed prairie dog based on Hall (1981), and complexes sampled (1 = Coyote Basin, sampled 27 May–18 Jun 1997; 2 = Moxa Arch, sampled 18–29 Jun 1997; 3 = Shirley Basin, sampled 30 Jun–16 Jul 1997).

(Fig. 1). Based on data from agency biologists, these 3 complexes also had the most recent and accurate colony location maps and contained the greatest number of large active colonies. Coyote Basin (Complex 1 in Fig. 1) was typical of the sagebrush-steppe of northeastern Utah and represented the extreme of brush-dominated white-tailed prairie dog habitat. Big sagebrush (*Artemisia tridentata*) and black greasewood (*Sarcobatus vermiculatus*) were the dominant overstory shrubs; exotic plants dominated the understory, especially cheatgrass (*Bromus tectorum*) and tumble mustard (*Sisymbrium altissimum*). This complex was planned as a future black-footed ferret (*Mustela nigripes*) reintroduction site. Moxa Arch (Complex 2 in Fig. 1) was a recently mapped complex and was within an active natural gas development field (Bureau of Land Management 1995). Colonies at Moxa Arch were smaller and more isolated. Habitat was typical of Wyoming Basin shrub-steppe: dominant plant species were low to moderate height shrubs such as Gardner saltbush (*Atriplex gardneri*) and big sagebrush. Common grasses were Sandberg bluegrass (*Poa secunda*) and Indian rice grass (*Oryzopsis contracta*). Shirley Basin (Complex 3 in Fig. 1) was a past black-footed ferret reintroduction site oc-

curing in the transition between shortgrass prairie and shrub-steppe. Vegetation was dominated by very low-growing shrubs, such as birdsfoot sage (*Artemisia pedatifida*) and Gardner saltbush, and by a mostly native grass-forb component of intermediate wheatgrass (*Agropyron intermedium*), phlox (*Phlox hoodii*), and woody aster (*Xylorhiza glabriuscula*). All 3 complexes occurred primarily on land administered by the Bureau of Land Management, were grazed by livestock (primarily cattle), were open to recreational prairie dog shooting, and had sylvatic plague in the prairie dog population. Sampling periods were 27 May–18 June 1997 at Coyote Basin, 18–29 June 1997 at Moxa Arch, and 30 June–16 July 1997 at Shirley Basin.

METHODS

Experimental Design

We sampled 74 prairie dog colonies (treatment replicate), using 1,444 artificial nests in a design that paired each colony with a nearby off site (control). To determine if habitat differences on and off colonies helped explain differences in predation rates, we estimated canopy cover, Robel cover (i.e., visual obscurity of vegetation; Robel et al. 1970), percent bare ground, and burrow density on each of the 74 colonies and their paired off sites. We also recorded type of nest disturbance for each predation event.

Colony Selection

Colonies were initially selected from maps prepared by agency biologists and sampled if they were a minimum size of approximately 500 × 1,000 m, had prairie dogs present or fresh scat (i.e., greenish black in color) at burrows, and access permission was obtained. Agency biologists had mapped colonies before our study began, typically by walking or driving colony perimeters with a Global Positioning System or by using a combination of aerial photographs, topographic maps, and ground-truthing. All colonies at each complex were sampled if they met these criteria and a suitable off site could be located. Paired on and off sites typically had similar livestock grazing, soil type, and topography. To locate off sites, we looked at colony boundaries to observe the type of habitat prairie dogs were colonizing and then searched nearby (usually 0.5–2.0 km) for similar sites lacking prairie dog colonies. Suitable off sites were sometimes difficult to find; if an off site could

not be found, the colony was not sampled. Some off sites contained a few scattered prairie dog burrows.

Vegetation–Burrow Density Data

We measured vegetation and burrow density along a single transect line in each of the 74 selected colonies and their paired off sites. Transects averaged 1,400 m long (range = 800–2,400 m). They began near the edge of a colony and continued through the center of prairie dog activity until the opposite side was reached (i.e., transect layout reflected colony shape and locations of active burrows). At off sites, we tried to mimic transect layout on paired colonies. We placed a pin flag every 100 m along transect lines and sampled vegetation with a Daubenmire plot (Mueller-Dombois and Ellenberg 1974) and Robel pole (Robel et al. 1970) placed 4 m from either side of the flag (2 plots and poles/flag). We recorded 4 readings (in cm from perpendicular locations) at each Robel pole location. On an average 1,400-m transect line, this method yielded 30 Daubenmire plots and 120 Robel cover estimates. We used the Daubenmire scale, as modified by Bailey and Poulton (1968), to estimate percent canopy cover of shrubs, grasses, forbs, litter, and bare ground at each 20- × 50-cm plot (Mueller-Dombois and Ellenberg 1974). In the analysis, we combined canopy cover measures into 2 categories: percent bare ground and percent vegetation cover (shrubs + grasses + forbs + litter). We estimated Robel cover (cm) by observing (from 1 m high and 4 m away) 1.5-m-tall Robel poles and recording the highest interval (marked in 2.5-cm increments) completely obscured by vegetation. Burrow density was estimated by recording the number of active prairie dog burrows within 1.5 m of a transect line (Biggins et al. 1993).

Nest Data

We placed artificial nests (\bar{x} = 9.75 nests/colony; \bar{x} = 9.75 nests/off site) 100 m apart along vegetation transect lines to compare predation rates on and off colonies. To aid nest relocation, we recorded compass direction and distance (4–15 m) from the transect line (marked with pin flags) to each nest location. We selected nest locations using a search image that represented likely nest sites for ground-nesting birds typical of the area (i.e., horned lark, McCown's longspur). This location was generally at the base of,

or within, a shrub, grass, or forb clump (With 1994, Beason 1995). We used the same search image on colonies and paired off sites. We scraped a shallow depression at each nest site and placed a single, fresh Japanese quail (*Coturnix japonica*) egg in it. These eggs were slightly smaller than mountain plover or killdeer eggs but were larger than those of horned larks or sparrows.

We placed equal (or nearly equal) numbers of nests on and off a particular colony on the same day, which ensured comparable exposure to predation across treatments. After an exposure time of t_1 days, nests were checked to determine if they had been disturbed. If eggs were found intact and logistical constraints permitted, eggs were left in the nest for an additional t_2 days and checked again for predation.

We recorded the condition of the nest scrape and egg each time it was checked to compare type of nest disturbance on and off colonies. We used 4 categories to analyze type of disturbance: none, egg moved but still intact, egg gone, and egg broken or crushed. We did not attempt to identify specific nest predators based on appearance of eggshell fragments, believing this technique leads to misidentification problems (Baker 1978, Hernandez et al. 1997).

Statistical Procedures

We compared nest predation on and off the 74 colonies by calculating daily predation probabilities for each colony \times site (on, off) combination and computing the difference in these probabilities for paired sites (i.e., $d = \text{Prob}_{\text{on}} - \text{Prob}_{\text{off}}$). A t -test of $H_0: \bar{d} = 0$ versus $H_a: \bar{d} > 0$ was computed for predation probability, differences in percent vegetation cover ($H_a: \bar{d} < 0$), differences in percent bare ground ($H_a: \bar{d} > 0$), differences in Robel cover ($H_a: \bar{d} < 0$), and differences in number of active prairie dog burrows per hectare ($H_a: \bar{d} > 0$). Because alternative hypotheses were specified a priori, we used 1-tailed tests. We used multiple regression to determine if measured habitat variables were good predictors of differences in predation rates. In this analysis, the difference in the daily predation probability was the dependent variable, and differences in percent vegetation cover, percent bare ground, Robel cover, and burrow density were the explanatory variables.

To calculate daily predation probabilities, we modeled the success or failure of a nest over an

interval, t , as an independent Bernoulli trial with parameter π_t . We then reparameterized π_t in terms of the daily survival probability to obtain the probability a nest succeeds or fails over t days:

$$P(Y = y|p) = (p^t)^y(1 - p^t)^{1-y},$$

where $y = 1$ if the nest succeeds, $y = 0$ if the nest is depredated, and p is the daily survival probability of the nest. Assuming that for the i th colony ($i = 1, \dots, 74$) daily survival probabilities for the on (p_i) and off (c_i) sites are homogeneous (i.e., colony \times site combinations are homogeneous), the likelihood function for the data is proportional to

$$\prod_{i=1}^{74} \prod_t (p_i^t)^{s_i}(1 - p_i^t)^{f_i}(c_i^t)^{s'_i}(1 - c_i^t)^{f'_i}, \quad (1)$$

where, for given i and t , s is the number of successful nests at the on site and s' is the number of successful nests at the off site, and f is the number of disturbed nests at the on site and f' is the number of disturbed nests at the off site. Estimators for p_i , c_i , and their variances were derived via standard maximum likelihood methods (Larsen and Marx 1986) and, for a given colony \times site combination, are equivalent to the estimators in Johnson (1979). Because closed-form solutions for these estimators do not exist, we used Newton's method to solve for the parameters (Swokowski 1988). Daily predation probabilities for on sites were computed as $1 - p_i$, and daily predation probabilities for off sites were computed as $1 - c_i$.

We also investigated various submodels of the colony \times site model in Equation (1) by constraining parameters to obtain simpler models. In particular, we imposed the constraint $p_i = c_i$, which assumes daily survival probabilities within a colony and its paired off site do not differ and constrained parameters so that daily survival probabilities within a complex \times site combination were homogeneous. According to Akaike's Information Criterion (AIC; Akaike 1973), the general model (1), which retains separate parameters for each colony \times site combination (i.e., $p_1, \dots, p_{74}, c_1, \dots, c_{74}$), was the most parsimonious model and should be used for parameter estimation (AIC = 2,651.1). This result is in agreement with likelihood-ratio tests, which rejected a submodel constraining $p_i = c_i$ ($\chi^2_{67} = 136.4, P < 0.001$; AIC = 2,659.1) and rejected the second model constraining colonies within a particular complex \times site combination

Table 1. On colony and off-site comparisons of type of disturbance to 1,444 artificial nests at 74 white-tailed prairie dog colonies in Colorado, Utah, and Wyoming, 1997.

Type of disturbance	On	Off	Total
None	337	393	730
Egg moved from nest but still intact	111	78	189
Egg gone without sign of disturbance	163	158	321
Egg broken or crushed, shell fragments in or near nest	111	93	204
Total	722	722	1,444

to have homogeneous nest survival probabilities ($\chi^2_{136} = 357.0$, $P < 0.001$; AIC = 2,718.9).

RESULTS

We summarized disturbance type for all 1,444 artificial nests and found eggs unmoved and intact at 730 nests (51%), moved but intact at 189 nests (13%), gone without sign of disturbance at 321 nests (22%), and broken or crushed at 204 nests (14%; Table 1). For purposes of estimating daily survival probabilities, nests with eggs unmoved and intact (730) were considered undisturbed (success; s or s' in Eq. 1), and all other nests (714) were considered disturbed (failure; f or f' in Eq. 1). The resulting daily survival probability estimates were used to test for differences in predation rates between on and off sites and were used to compute 14-day predation rates (%) to mimic an incubation period typical of grassland and shrub-steppe birds.

Differences in daily predation rates between on and off sites averaged $1.0 \pm 0.6\%$ ($\bar{x} \pm \text{SE}$;

$t_{73} = 1.57$, $P = 0.060$). When converted to 14-day rates, nest predation averaged 14% higher on colonies ($\bar{x} = 57.7 \pm 2.7\%$) than at off sites ($\bar{x} = 50.4 \pm 3.1\%$). For vegetation and burrow density data, we found mean differences were $-3.1 \pm 2.5\%$ ($t_{73} = -1.21$, $P = 0.114$) for vegetation cover, $6.0 \pm 1.9\%$ ($t_{73} = 3.09$, $P < 0.001$) for bare ground, $-3.0 \pm 0.6 \text{ cm}$ ($t_{73} = -4.66$, $P < 0.001$) for Robel cover, and 94.2 ± 6.2 burrows/ha ($t_{72} = 15.27$, $P < 0.001$) for density of active prairie dog burrows. There was less available nesting cover and more prairie dogs on colonies than at nearby off sites. These patterns were generally consistent across all 3 complexes (Table 2). Interestingly, the difference in mean 14-day nest predation was greatest (12.7%) at the Moxa Arch complex in southwestern Wyoming, where vegetation cover was the lowest and bare ground the highest both on and off colonies. However, regression analysis showed that none of the 4 explanatory variables we tested was useful as a predictor of differences in nest predation rates on and off colonies ($P_s > 0.288$ for all variables).

Eggs were moved from the nest (often about 15 cm) but still intact at 111 nests on colonies and 78 nests at off sites (Table 1). These data suggest moved but intact eggs strongly influenced our finding that nest predation was higher on colonies. Because nesting birds may not recognize or incubate an egg moved from their nest, the usual method in nest predation studies is to consider these nests as disturbed. In our study, however, we believed prairie dogs may have moved eggs without trying to eat them, possibly a result of curiosity about something

Table 2. On colony and off-site comparisons of 14-day nest predation rates and habitat variables at 3 white-tailed prairie dog complexes in Colorado, Utah, and Wyoming, 1997.

Variable	Site	Complex					
		Coyote Basin ($n = 31$)		Moxa Arch ($n = 9$)		Shirley Basin ($n = 34$)	
		\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
14-day nest predation (%) ^b	On	47.7	4.1	60.7	9.6	66.0	3.2
	Off	42.6	4.7	48.0	12.2	58.0	3.7
Vegetative cover (%)	On	59.2	4.2	34.4	3.7	56.4	1.6
	Off	59.2	3.6	39.8	3.9	60.8	2.8
Bare ground (%)	On	50.6	2.9	77.3	2.1	48.2	2.2
	Off	45.6	2.5	65.9	3.3	43.3	2.4
Robel cover (cm)	On	3.3	0.5	1.5	0.3	0.4	0.1
	Off	9.3	1.8	2.7	0.4	1.4	0.4
Active burrows (burrows/ha)	On	76.1	7.2	98.5	18.7	116.1	9.2
	Off	0.2	0.1	1.4	1.4	0.7	0.3

^a n = number of colonies sampled.
^b Calculated from daily survival probabilities.

new to their territory. Because this response may not have occurred with natural nests, we reanalyzed the data by combining the 189 moved but intact nests with the 730 survived nests and considered these 919 nests as undisturbed (success; s or s' in Eq. 1). Using these categories, we found that nest predation did not differ between on and off sites ($d = 0.2 \pm 0.5\%$; $t_{73} = 0.34$, $P = 0.369$). Mean 14-day predation rates were $44.8 \pm 2.7\%$ at colonies and $41.6 \pm 3.0\%$ at off sites.

DISCUSSION

Prairie Dogs as Nest Predators

Prairie dogs have been reported as potential nest predators, but without supporting data (Mickey 1943, With 1994). Prairie dogs might reasonably be assumed to prey on bird eggs because thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) and related species are known nest predators (With 1994) and because prairie dogs scavenge animal carcasses and cannibalize their young (Hoogland 1995). However, if prairie dogs regularly eat bird eggs, then nest predation should be much higher on colonies, even higher than the 7% difference we observed. Mean prairie dog density at our 3 complexes was about 7.1/ha on colonies and 0.5/ha at off sites (no. of prairie dogs = $0.073 \times$ number of active burrows; Biggins et al. 1993), suggesting eggs on colonies were at high risk of detection by prairie dogs. Even eggs placed near active burrows often were not damaged, indicating at least some prairie dogs ignored eggs they clearly must have found. We did find more nests with eggs moved but intact on colonies (Table 1), suggesting prairie dogs may have at least been curious about eggs in their territory. However, these moved but intact eggs also may have been unsuccessful predation attempts by other small mammals (e.g., deer mice), which also may be more abundant on colonies (Agnew et al. 1986). However, without predator identification data, conclusions drawn from circumstantial evidence in our study could be incorrect. Research that identifies predators at nests is clearly needed before we implicate prairie dogs as nest predators.

Nest Predation Differences

A variety of potential nest predators could have been responsible for the increase in predation rates we observed on colonies. Krueger (1986) reported that badgers and coyotes were

more abundant on than off black-tailed prairie dog (*C. ludovicianus*) colonies. We observed both of these predators, as well as swift foxes, striped skunks (*Mephitis mephitis*), and long-tailed weasels (*Mustela frenata*) on or near colonies at our study sites. However, we found similar numbers of eggs missing and broken on and off colonies (Table 1), which are the 2 most likely methods of egg destruction by these predators (Baker 1978, Hernandez et al. 1997). These data suggest the relative importance of medium-sized mammalian nest predators may have been similar on and off colonies. Deer mice and grasshopper mice, both potential nest predators at our colonies, also were more abundant on than off colonies at Badlands National Park in South Dakota (Agnew et al. 1986). These and other small mammals may have been responsible for some of the differential predation, or attempted predation (i.e., moved but intact eggs), we observed on and off colonies.

We also expected vegetation height and density to influence nest predation. Because Robel cover blends both metrics into 1 measure (Robel et al. 1970), it is often a good predictor of nesting habitat for grassland birds. At our study sites, we found that Robel cover was lower on colonies, but that it was not a good predictor of predation differences in the multiple regression analysis. However, the magnitude of the difference was small, as cover averaged only 3 cm less on colonies than at off sites. Perhaps this small difference was not meaningful to nest predators. Robel cover also may be a better predictor of nest predation for black-tailed prairie dogs, where the contrast on and off colonies is greater than for white-tailed prairie dogs (Hoogland 1995). In addition, livestock grazing may minimize differences between colonies and nearby off sites, regardless of the prairie dog species in question.

Compensation for Higher Nest Predation on Colonies

Even a 14% increase in 14-day predation rates, as we observed in our study, would likely suppress recruitment of birds into the local population. But why would birds nest on prairie dog colonies if the risk of nest predation is higher? We offer the following thoughts as speculation. Coevolution of nesting birds and prairie dogs occurred when colonies and complexes were much larger, and before fragmentation diminished their relative area. Perhaps before col-

onies were fragmented, the risk of predation was not higher for birds nesting on colonies. However, recent fragmentation of prairie dog complexes into smaller and smaller colonies may have created "predator patches," unique features of the landscape that stand out from the surrounding matrix and create conditions that increase local predation rates. Colonies that function as predator patches may increase predator density (potentially increasing both primary and secondary nest predation) and allow predators to develop a more narrow and successful search image. In effect, fragmentation of prairie dog habitat may function similar to fragmentation of waterfowl nesting habitat in the Prairie Pothole Region, where nest predation rates of about 70% may limit waterfowl production (Greenwood et al. 1995). Fragmentation may be more important for black-tailed prairie dogs, where habitat loss on private lands has been severe. In contrast, white-tailed prairie dogs occur mostly on public rangelands, where control efforts have been less and the landscape still resembles historical conditions.

Under current conditions, species that evolved close associations with prairie dogs might compensate for increased predation by having increased relative fitness, perhaps through foraging efficiency or fledgling survival. Many birds associated with prairie dogs forage by walking on the ground, picking up insects or vegetative material as they move (e.g., McCown's longspur [With 1994], horned lark [Beason 1995]). At the Shirley Basin complex, we observed flocks of up to 40 juvenile horned larks foraging on colonies in this manner. Because there is less vegetation and more bare ground, foraging also may be more efficient on colonies than off (e.g., mountain plover; Olson 1985). In addition, insect species important to foraging birds may be more numerous on colonies (Olson 1985). Even if nest predation is significantly higher on colonies than surrounding habitat, the implications to fitness of local bird populations is uncertain. Clearly, more research is needed, especially on the interaction of avian fitness with spatial patterns of prairie dog abundance.

MANAGEMENT IMPLICATIONS

Many species associated with prairie dogs are declining in concert with the continued decline of prairie dogs. However, these associates have evolved to prefer nesting conditions on colo-

nies. Therefore, any effect of slightly higher nest predation on colonies likely would not be a serious concern for managers, at least for white-tailed prairie dogs; however, the implications for other species are unclear. Because of habitat and behavioral differences, our results may not apply to the other 4 species of prairie dogs. We recommend further research on those species and their associated avifauna, especially where prairie dog control, habitat loss, or sylvatic plague threatens to further fragment remaining complexes. We also recommend further research on the role of prairie dogs as nest predators.

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